ARTICLE

Nontarget impacts of insecticide-based population control of eastern spruce budworm (Lepidoptera: Tortricidae) on nontarget caterpillar communities and parasitism

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Abstract

Narrow-spectrum insecticides are currently used to control populations of spruce budworm, *Choristoneura fumiferana* Clemens (Lepidoptera: Tortricidae), in eastern Canada. However, these could have nontarget impacts on other caterpillars – some of which may serve as alternative or alternate hosts to key parasitoids – that are also susceptible to control tactics. This study was conducted to determine how the insecticides, *Bacillus thuringiensis* variety kurstaki (*Bt*k) and tebufenozide, used to control spruce budworm populations, impact caterpillar communities and associated parasitism rates. Post-treatment field sampling of caterpillars was conducted in 2018 and 2019 in New Brunswick, Canada, at sites treated with either *Bt*k or tebufenozide and at control sites. Caterpillar species richness and abundance, community structure, and parasitism rates were assessed using molecular analyses for 659 collected caterpillars. We found that insecticide applications had no significant impact on abundance, species richness, or parasitism rate relative to the measurements made in the control sites. Nonetheless, a significantly higher caterpillar abundance and lower parasitism rate occurred in *Bt*k-treated sites than in tebufenozide-treated sites. Overall, however, *Bt*k and tebufenozide treatments did not negatively affect the non-budworm caterpillar community under the present conditions of low caterpillar densities, suggesting that parasitoids have alternative and alternate hosts after treatments that target the spruce budworm.

Introduction

Insecticides are commonly used to control pests in forestry and agriculture (Sharma *et al.* 2019). However, because of concerns about their potential impacts on both the environment and human health, the number of registered pesticides has declined over the past 40 years in Canada (Holmes and MacQuarrie 2016). For example, in the 1950s, the major forest pest spruce budworm, *Choristoneura fumiferana*, Clemens (Lepidoptera: Tortricidae), was controlled using the broad-spectrum insecticide dichlorodiphenyltrichloroethane (DDT), and in the 1970s, DDT was replaced by fenitrothion. However, these insecticides were

controversial even at the time they were used and elicited strong public concern, as reported in two well-known books: *Silent Spring* (Carson 1962) and *Budworm Battles* (May 1982). Although there has been a general shift away from broad-spectrum insecticides towards tactics that more narrowly affect target species, studying insecticides' impacts on nontarget species remains an essential step towards the development of sound pest management strategies (Desneux *et al.* 2006; Siviter and Muth 2020; Leroy *et al.* 2022).

Spruce budworm outbreaks occur throughout the Canadian boreal forest, where it is one of the most intensively managed forest pests (Canadian Council of Forest Ministers 2022). It is a native outbreaking species feeding on buds of balsam fir, *Abies balsamea* (Linnaeus) Miller (Pinaceae), and spruces, *Picea* spp. (Pinaceae) (MacLean 1984). Outbreaks occur at roughly 30- to 40-year intervals (Boulanger and Arseneault 2004), with each outbreak lasting as long as 10–15 years (Boulanger *et al.* 2012). The outbreaks can affect ecosystem services (Schowalter 2012) and adversely affect nontargeted Lepidoptera (Scriber 2004), in addition to having important economic impacts resulting from tree growth reductions and mortality (MacLean and Ostaff 1989; Chang *et al.* 2012).

The spruce budworm supports a complex trophic network of more than 100 different parasitoid and hyperparasitoid species (Eveleigh *et al.* 2007). Although several factors influence spruce budworm population dynamics, predator–prey dynamics involving these parasitoids are the major factor in driving the budworm's outbreak cycles (Royama 1984; Eveleigh *et al.* 2007; Régnière and Nealis 2007). These parasitoids also play an important role during periods between outbreaks by maintaining populations at almost imperceptibly low densities (Bouchard *et al.* 2018; Régnière *et al.* 2019). Additional factors that regulate budworm populations include viruses, birds predation, food depletion, and climate (Régnière and Duval 1998; van Frankenhuyzen *et al.* 2007; Pureswaran *et al.* 2016; Régnière *et al.* 2021).

A spruce budworm outbreak has been occurring in the province of Québec, Canada, since 2006, affecting more than 12 million hectares of spruce and fir forests as of 2021 (Ministère des Forêts de la Faune et des Parcs 2021). In response to the risk of this outbreak expanding south throughout Atlantic Canada, forest managers in New Brunswick have adopted a novel population control strategy, the so-called "Early Intervention Strategy" (Johns *et al.* 2019). This strategy involves detecting and controlling low-density budworm populations as they begin to increase (*i.e.*, "hotspots") at the leading edge of an outbreak to prevent further increase and spread, leading to insecticide treatments being applied at lower population densities than have been targeted historically (Johns *et al.* 2019). At the time of the present study, the only budworm control products registered in Canada were *Bacillus thuringiensis* Berliner serotype kurstaki (*Bt*k) and tebufenozide, both of which are specific to caterpillars (Durkin 2004; Durkin and Klotzbach 2004). The half-life of *Bt*k on spruce needles varies from 12 hours to a few days (Sundaram *et al.* 1994, 1996a), and the half-life of tebufenozide varies from 20 to 45 days (Sundaram *et al.* 1996b), depending on the application parameters (Moreau and Bauce 2003). Due to how these insecticides act on caterpillars – a mode that requires ingestion – other nontarget caterpillars that are feeding at the same time as spruce budworm and on the same treated foliage might also be affected.

Nontarget impacts from treatments could negate the potential benefits of the Early Intervention Strategy approach. Insecticide application can potentially affect all species of caterpillars that are present on foliage during a product's effective period, including alternate and alternative hosts – some of which could be harbouring spruce budworm parasitoids (Cappuccino *et al.* 1998; Pfannenstiel *et al.* 2010). Such nontarget effects could even promote spruce budworm population growth in subsequent years by reducing the action of the parasitoids due to a lack of alternative hosts, through a mechanism called "apparent competition" (Holt and Lawton 1993). Nontarget impacts of *Bt*k and tebufenozide on the caterpillar community have been documented previously, potentially reducing species richness and abundance (Miller 1990; Butler *et al.* 1997; Rastall *et al.* 2003; Boulton *et al.* 2007).

Although parasitoid populations could be affected by this reduction of host numbers, parasitised larvae are known to feed less (Nealis and van Frankenhuyzen 1990). Therefore, developing parasitoids within a host are less likely to be directly affected by an insecticide treatment.

The goal of the present study was to assess whether *Bt*k and tebufenozide, when applied on low-density budworm populations, affect the species abundance and richness and the community structure of the nontarget caterpillar community (*i.e.*, species that are not spruce budworm), as well as associated parasitism rates.

Materials and methods

Field surveys of caterpillars were conducted in treated and neighbouring untreated areas in the year of treatment (2018) and one year after treatment (2019), thus allowing assessment of immediate and lingering impacts.

Study sites

Study sites were located in northeastern New Brunswick, Canada, within areas where insecticide applications from Early Intervention Strategy treatments were conducted between 9 June and 30 June 2018 (Fig. 1; Table 1). The insecticides were applied once in the season by aircraft, at a rate of 30 billion international units per litre in 1.5 L/ha for the *Bt*k (Foray 76B, Valent BioSciences, Guelph, Ontario, Canada) and at a rate of 70 g active ingredient in 1.5 L/ha for the tebufenozide (Limit 240, Spray Industries, Saint John, New Brunswick, Canada), when larvae were between their third and fourth instars. Five sites were selected within each of the *Bt*k and tebufenozide treatment blocks (totalling 10 treated sites), and five sites were selected in nearby zones that received no insecticide treatment (control sites). Treated sites were located more than 150 m from the treatment block borders, and control sites were located more than 1 km away from treated areas. All sites were selected to have a similar composition: they were dominated by fir and spruce trees (50–75%), and the most abundant deciduous tree species were paper birch, *Betula papyrifera* Marshall (Betulaceae), maple, *Acer* spp. Linnaeus (Sapindaceae), and aspen, *Populus* spp. Linnaeus (Salicaceae). A complete list of deciduous species sampled among sites can be found in Supplementary material, Table S1.

Caterpillar sampling

Sampling was conducted at all 15 sites for two consecutive years – that is, in 2018 (the year of insecticide applications) and in 2019 (one year after treatment, with no additional insecticide application occurring). The sites were visited four times each year, from mid-June to September. In order to sample as many niches as possible, three sampling techniques were used: branch collection, branch beating, and visual inspection. To sample caterpillars from the canopy, five deciduous trees and 15 conifers (fir or spruce), with heights between 15 and 20 m, were randomly selected at each visit, depending on their relative abundance. One 45-cm-long branch was cut from the mid-crown of each conifer and deciduous tree, using a pole pruner equipped with a basket attachment to collect any falling insects. The branches were placed in paper bags, transported to the laboratory, and kept at 4 °C until they were processed in the laboratory. During processing, caterpillars were collected from each branch and stored individually in ethanol (70%) at 4 °C. Branch beating and observation were conducted along two 50-m transects at each site. Using a stick, every plant and branch within a 2-m-wide × 2-m-high section along the transect was beaten three times to collect insects falling onto a piece of white fabric (90 cm diameter; BugDorm #211210; MegaView Science Co., Ltd., Taiwan) that had been placed underneath the plant. Afterwards, visual inspection was conducted along the same transect for caterpillars on all types of vegetation,

Table 1. Sampling dates for the year of *Bt*k and tebufenozide treatments (2018) and one year following treatment (2019).

Sampling	2018	2019
1	25–29 June	25–29 June
2	10–14 July	22–25 July
3	7–11 August	12–15 August
4	20–24 September	16–19 September
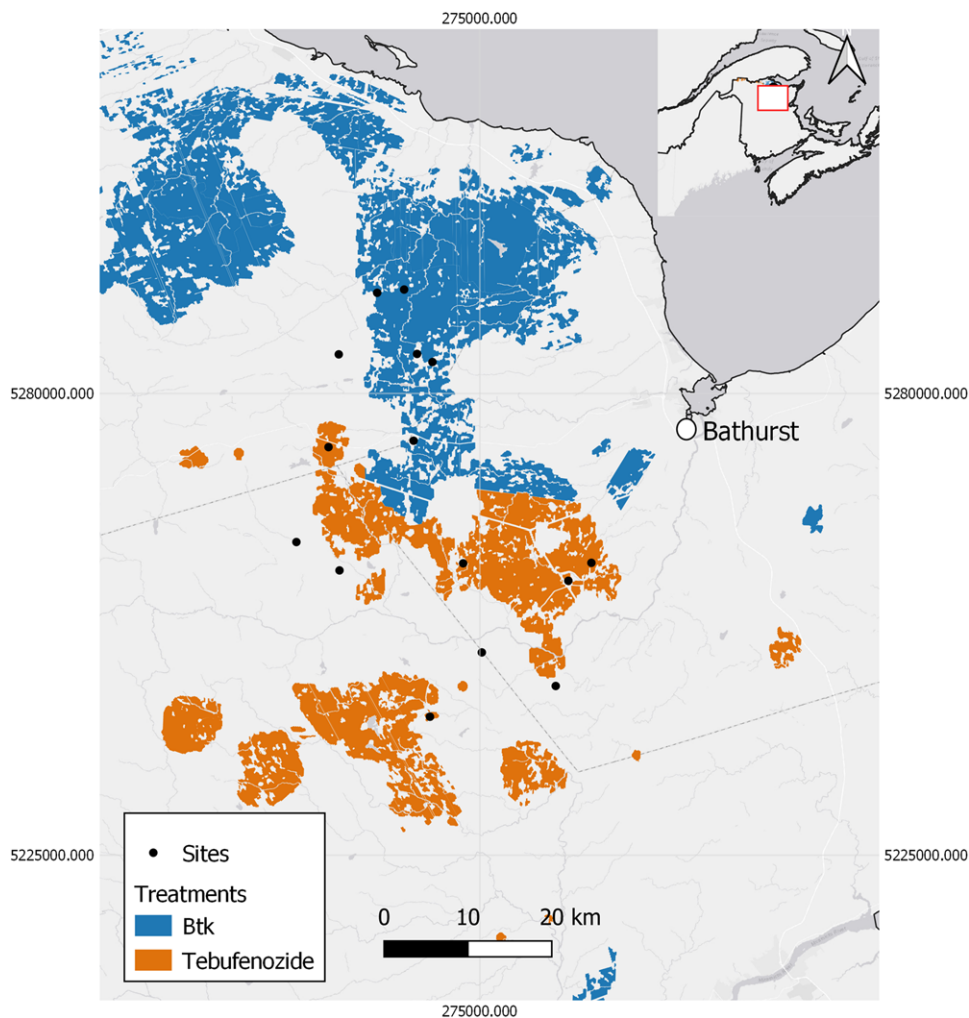
Fig. 1. Sites sampled in New Brunswick, Canada, during the year of the insecticide treatments (2018) and one year after treatment (2019).

including bark, rolled leaves, branches, and so on. The time allotted to each inspection varied according to vegetation density but never exceeded 20 minutes per transect. All caterpillars found during branch beating and observations were stored individually in ethanol (70%) at 4 °C. New transects were positioned a few metres away from the previous ones at each visit to prevent sampling of damaged or depleted plants.

Molecular analyses

To determine whether the sampled caterpillars were parasitised, we used the quantitative polymerase chain reaction–based molecular sorting tool developed by Nisole *et al.* (2020), which enabled detection of hymenopteran and dipteran DNA within each individual caterpillar. All polymerase chain reaction–positive samples were considered parasitised. For caterpillar species identification, polymerase chain reaction amplifications of the mitochondrial cytochrome c oxidase 1 gene (*CO*1) were conducted on a PTC-100 thermocycler (MJ Research, Watertown, Massachusetts, United States of America), targeting the lepidopteran species, following the procedure of Djoumad *et al.* (2017) but using only 0.2 U of Platinum SuperFi DNA polymerase (Invitrogen, Waltham, Massachusetts) and employing a universal set of primers that targeted a 710-bp *CO*1 fragment (primers LCO1490 and HCO2198, following Folmer *et al.* 1994). Polymerase chain reaction products underwent Sanger sequencing at the Plateforme de séquençage et de génotypage des génomes, Centre hospitalier de l'Université Laval (City of Québec, Québec, Canada). Species were identified using the Basic Local Alignment Search Tool (BLAST) against the National Center for Biotechnology Information nonredundant database (Madden 2002).

Statistical analyses

All analyses were done in R, version 4.0.5 (R Core Team 2021). Preliminary analyses were carried out to verify if conifer relative abundance (percentage of stand composition), plant richness, and latitude affected the caterpillar species abundance or richness or the parasitism rate using the AICcmodavg package, version 2.3.1 (Mazerolle 2020; Supplementary material, Table S2). Because none of these variables had a significant effect, these parameters were removed from the final models.

To examine the effects of insecticide treatment on caterpillar richness, a generalised linear mixed-effects model (family = Poisson; link = log) was used, which was fit using the *glmer* function from the lme4 package, version 1.1.27.1 (Bates *et al.* 2015). Year, treatment, year × treatment interaction, and month of sampling were included as fixed effects, and site was fit as a random effect. To account for potential differences in sampling effort, the number of plants beaten per transect was included as an offset (log-transformed, following Roback and Legler 2021). To determine the effects of insecticide treatments on nontarget species (*i.e.*, non-budworm caterpillars), the total abundance of nontarget caterpillars was modelled using a negative binomial generalised linear mixed-effects model using the *glmer.nb* function from the lme4 package. The same model parameters (fixed effects, random effects, and offset) were used as described above. However, in this model, the highest spruce budworm abundance estimated during the summer was included as a covariate to account for potential interspecific competition between spruce budworm and other species of caterpillars that also feed on spruce and fir during the season. For each generalised linear mixed-effects model, the significance of fixed effects was determined using the *drop1* function, which compares all models that can be made by dropping a single model (Zuur *et al.* 2009). When main effects were significant, *post hoc* pairwise comparisons were conducted using the *emmeans* function from the emmeans package, version 1.7.2 (Lenth *et al.* 2022).

To determine if caterpillar communities differed among the treatment groups, a permutational multivariate analysis of variance was conducted, using the package pairwiseAdonis, version 0.4 (Martinez Arbizu 2020), with 999 permutations of the data. Each permutational multivariate analysis of variance was followed by nonmetric multidimensional scaling (NMDS) ordination to visualise the data. The NMDS was run with a matrix of the log-transform ($\log(x + 1)$) abundance of each caterpillar species per site and pooled per year and with a Bray–Curtis dissimilarity calculation with the *metaNMDS* function of the vegan package, version 2.5.7 (Oksanen *et al.* 2020). For the year of the treatment, data were pooled according to early season (first and second sampling) or late season (third and fourth sampling) because the delay of insecticide residues over time could mediate different responses between seasonal assemblages. The following year, because a smaller number of caterpillars was collected, the data could not be pooled according to early or late season, and the communities sampled from the entire season were therefore analysed together.

The effects of treatments on parasitism rates were assessed using a binomial generalised linear mixed-effects model that was fit using the *glmer* function (family = binomial; link = logit) from the lme4 package. The dependent variable was a two-column matrix containing the numbers of parasitised caterpillars and of nonparasitised caterpillars. Model parameters included year, treatment, year × treatment interaction, and month of sampling as fixed effects, site as a random effect, and spruce budworm abundance as a covariate. A significant year × treatment interaction ($P = 0.001$) made it difficult to interpret treatment effects; for this reason, the same model was built for each year separately. The *Anova* function (with type = 3) from the car package (Fox and Sanford 2019) was used to test for significance of fixed effects. *Post hoc* tests were conducted on the significant parameters with the *emmeans* function from the emmeans package.

Results

Caterpillar richness and abundance

A total of 744 caterpillars were collected, with 419 being sampled in 2018 and 325 being sampled in 2019. The genera of all specimens were successfully identified, and 623 specimens were further identified to the species level. Overall, 82 different species of caterpillars from 13 different taxonomic families were inventoried (Supplementary material, Table S3).

Although neither year on its own nor the interaction between treatment and year significantly impacted species richness (*i.e.,* the number of species sampled), both treatment and sampling month significantly affected this variable (Table 2). None of the samples from either of the insecticide treatments had significantly different species richness compared to the control, but samples collected in *Bt*k-treated sites displayed significantly higher caterpillar species richness than did those collected in tebufenozide-treated sites ($P = 0.012$; Fig. 2A). Species richness also showed seasonal variation, with species richness being higher in September compared to in previous months ($P < 0.001$; Fig. 3A).

Treatment, year, spruce budworm abundance, and the interaction between year and treatment had no significant impact on caterpillar abundance, but sampling month did have a significant impact (Table 2; Fig. 2B). Samples collected in September displayed significantly higher abundance than those collected earlier ($P < 0.001$; Fig. 3B).

Caterpillar community

In early-season 2018, during which the first two samplings of the season were collected, the composition of caterpillar species communities differed significantly between *Bt*k-treated and tebufenozide-treated sites ($P = 0.01$; Table 3), with treatment type explaining 27.15% of the

Table 2. Statistical values from the generalised linear mixed-effect models explaining the caterpillar species richness (number of species), abundance, and the associated parasitism rate, for both years combined and separated. Significant *P*-values are shown in bold font.

Models	Fixed effects	d.f.	F	P
Richness	Treatment	2	5.084	**0.025**
	Year	1	5.343	0.065
	Treatment: year	2	1.836	0.399
	Sampling month	4	11.925	**< 0.001**
Abundance	Treatment	2	5.744	0.134
	Year	1	4.107	0.958
	Treatment: year	2	1.738	0.419
	Sampling month	4	21.103	**< 0.001**
	Spruce budworm abundance	1	3.245	0.067
Parasitism rate	Treatment	2	1.184	0.232
	Year	1	5.727	0.084
	Treatment: year	2	6.655	**0.001**
	Sampling month	4	8.958	**< 0.001**
	Spruce budworm abundance	1	19.435	**< 0.001**
Parasitism rate 2018	Treatment	2	0.558	**0.036**
	Sampling month	3	5.299	**0.002**
	Spruce budworm abundance	1	11.490	**0.002**
Parasitism rate 2019	Treatment	2	1.323	0.775
	Sampling month	4	5.911	**< 0.001**
	Spruce budworm abundance	1	18.368	**< 0.001**

variability between the two communities (stress value = 0.117; Fig. 4A). No other comparisons were significant. In late-season 2018, when the two last samplings of the season occurred, community composition also differed significantly between *Bt*k-treated and tebufenozide-treated sites ($P = 0.05$; Table 3), with treatment type explaining 20.2% of the variability between the two communities (stress value = 0.100; Fig. 4B). Again, no other comparisons were significant. For samples collected in 2019, no significant differences among all three treatments were detected in caterpillar species communities (stress value = 0.176; Fig. 4C; Table 3).

Parasitism rates

Of all the caterpillars collected, 44.7% of the 41 lepidopteran species were parasitised. Of these parasitised caterpillars, 75.2% were parasitised by a hymenopteran, 11.9% by a dipteran, and 12.9% by both (Supplementary material, Table S1).

The interaction between treatment and year, sampling month, and spruce budworm abundance had significant impact on parasitism rates, whereas treatment and year alone had no impact (Table 2). Parasitism rates were observed to be higher in September than in earlier months ($P < 0.001$) and were also higher when spruce budworm was abundant ($P < 0.001$). As the interaction between treatment and year was significant ($P = 0.001$), the data were
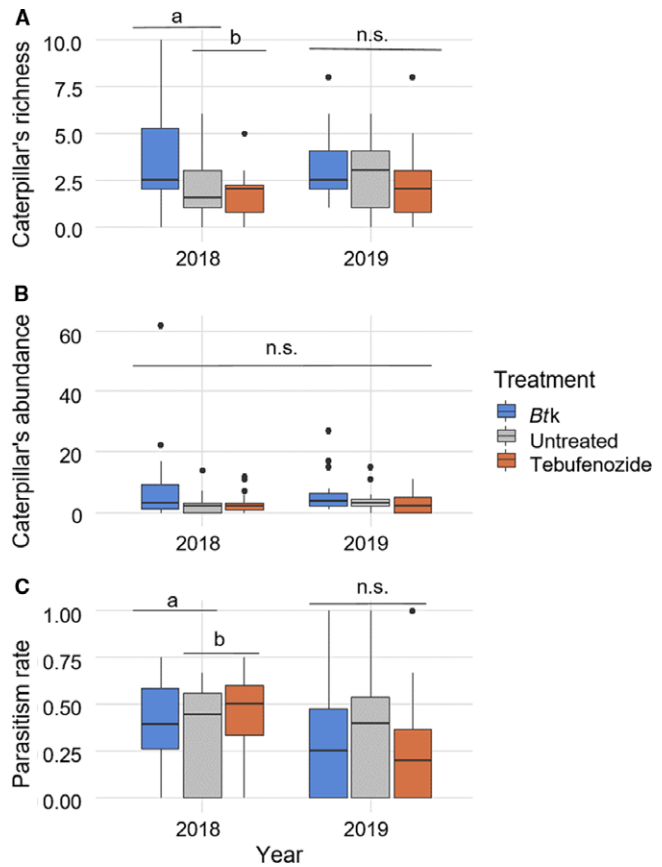
Fig. 2. A, Nontarget caterpillar richness (number of species), **B**, abundance, and **C**, parasitism rates per treatments in New Brunswick, Canada. Insecticides were applied in 2018 only but were sampled in 2018 and 2019. Different letters indicate significant differences from *post hoc* test applied when an effect of treatment was detected, and parasitism rates were analysed per year.

analysed for each year individually. In 2018, treatment, sampling month, and spruce budworm abundance had a significant impact on parasitism rates (Table 2): parasitism rates were higher in September (Fig. 3C) and when spruce budworm was abundant. A *post hoc* test revealed a significantly higher rate of parasitism in tebufenozide-treated than in *Bt*k-treated sites ($P = 0.022$), whereas the rates for control sites did not significantly differ from those of treated sites (Fig. 2). In 2019, treatment had no significant impact on parasitism rates, but both sampling month and spruce budworm abundance significantly affected parasitism rates. Parasitism rates were higher in September (Fig. 3C) and when spruce budworm was abundant.

Discussion

Treatment neither with *Bt*k nor with tebufenozide significantly affected species abundance, species richness, or community composition relative to control sites under the conditions tested. Different studies have shown different impacts of insecticide treatments on caterpillar communities, with some reporting negative impacts and others reporting positive impacts. For example, Westwood *et al.* (2019), who sampled the Lepidoptera community following a tebufenozide treatment against spruce budworm, showed a reduction in abundance of some species. However, this study was conducted in high-density spruce budworm populations subjected to higher application rates (*i.e.,* 70 g active ingredient in 20 L/ha). Comparable past studies reported a reduction in caterpillar richness and abundance following *Bt*k or tebufenozide application against the spongy moth, *Lymantria dispar dispar* (Linnaeus) (Lepidoptera: Erebidae) (Miller 1990;

Table 3. Results of the pairwise permutational multivariate analysis of variance (999 permutations of the data) conducted on the composition of the caterpillar community between each type of treatment. Significant *P*-values are shown in bold font.

| Period	Treatment comparison	R^2	F	P
Early 2018	*Btk versus* tebufenozide	0.271	2.979	**0.01**
	Btk versus control	0.173	1.468	0.152
	Tebufenozide *versus* control	0.177	1.503	0.131
Late 2018	*Btk versus* tebufenozide	0.202	2.028	**0.05**
	Btk versus control	0.206	2.070	0.063
	Tebufenozide *versus* control	0.171	1.644	0.142
2019	*Btk versus* tebufenozide	0.110	0.988	0.498
	Btk versus control	0.106	0.945	0.530
	Tebufenozide *versus* control	0.165	1.576	0.067
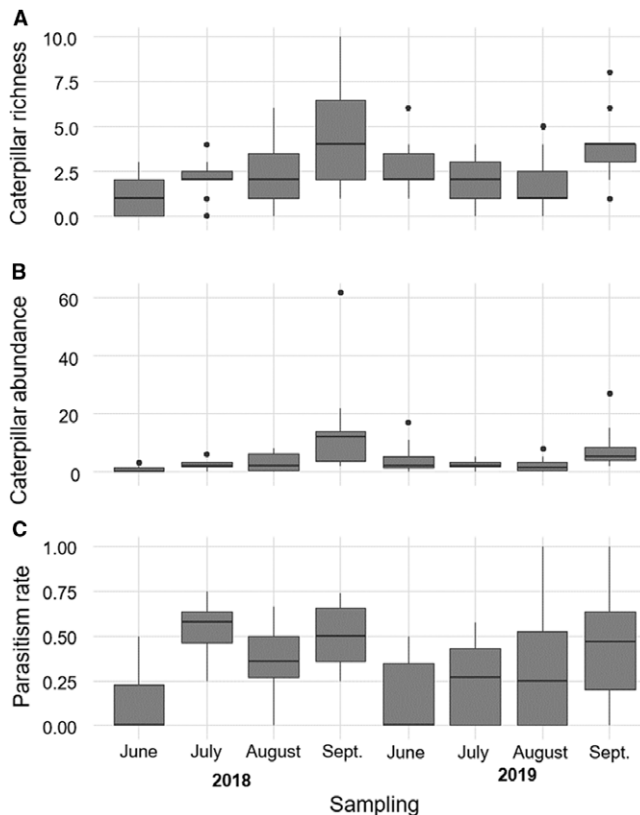
Fig. 3. A, Caterpillar richness and **B**, abundance and **C**, parasitism rate for each sampling month, from May to September, in 2018, the year of the treatment, and in 2019, the year following the treatment.

Wagner *et al.* 1996; Butler *et al.* 1997; Rastall *et al.* 2003; Boulton *et al.* 2007). However, in those studies, too, insecticide concentrations were higher than what was used in the present study, and because the sampled plant species were mostly deciduous, they supported a higher biomass and greater diversity of caterpillars than coniferous trees do (Southwood *et al.* 2004).
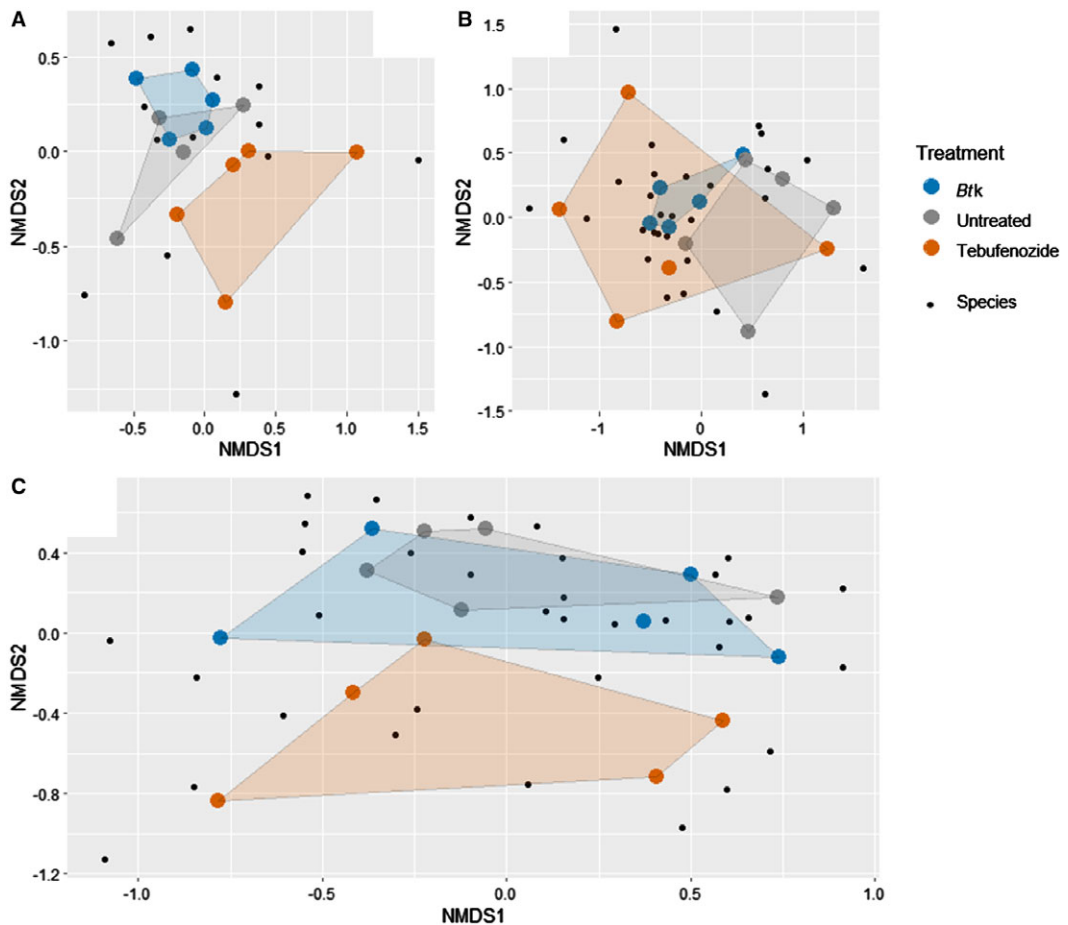
Fig. 4. Ordination plot (NMDS, $k = 2$) with Bray–Curtis dissimilarity matrix on the caterpillar community, **A**, during early season in the year of the treatment (stress value: 0. 117); **B**, during late season in the year of treatment (stress value: 0.100); and **C**, one year after treatment (stress value: 0.176).

The numbers of caterpillars collected in treated and untreated sites in the present study were lower than expected, which could explain the differences in results that the aforementioned earlier studies found. The same type of sampling, with the same protocol, was conducted on other sites studied for spruce budworm in Québec, and the caterpillars were found to be approximately twice as abundant (Valentine Glaus, unpublished data). This could be explained by the diversity of plants, mainly understorey plants because they can host numerous caterpillars, by geographical differences, or by the spruce budworm population density. Large stochastic variations in Lepidoptera abundance (Myers 1988; Raimondo *et al.* 2004) could also explain the low sample size: at low caterpillar abundance, the effect of insecticide may be diluted, which might explain the absence of effect. The low number of caterpillars collected in the present study prevented us from doing individual species analyses or analysing the effect of the treatment throughout the season.

In contrast, other studies have reported positive impacts of *Bt*k treatments on nontarget caterpillar species. For example, *Bt*k seemingly protected geometrid species from the negative impacts of spongy moth–induced defoliation (Sample *et al.* 1996; Manderino *et al.* 2014). Scriber (2004) argued that a *Bt*k treatment might have a less of an impact on the caterpillar species community than an outbreak caused by a major defoliator would. A rise in species

richness following *Bt*k application could thus be explained by a reduction in the population levels of an outbreaking species, which might increase the available foliage (Redman and Scriber 2000), decrease the production of pest-induced plant defence compounds (Kosola *et al.* 2001; Fuentealba and Bauce 2016), or increase parasitoid abundance (Holt and Lawton 1993; Redman and Scriber 2000). Although tebufenozide also suppressed the population of an outbreaking species, this insecticide has a substantially longer half-life than *Bt*k does (Sundaram *et al.* 1996a, 1996b), which might explain tebufenozide having no significant positive impact on nontarget caterpillar species richness. It should be pointed out here that the spruce budworm population densities targeted under the Early Intervention Strategy are below levels that would cause significant inter- or intraspecific competition, and therefore, the impact of removing the outbreaking species might not be as important as it was in other studies.

Results from the present study pointed to higher caterpillar species richness in *Bt*k-treated sites compared to tebufenozide-treated sites. A difference in community composition between the treatments was also detected in the year of the treatment, both early and late in the season. This may be explained by differences in the half-lives of the two insecticides used, with *Bt*k having a half-life of 12 hours to a few days and tebufenozide having a half-life of 20–45 days (Sundaram *et al.* 1996a, 1996b). Although a significant difference in caterpillar species richness between the *Bt*k-treated sites and the tebufenozide-treated sites remained one year after treatment, the corresponding difference in community composition had disappeared in that time.

The phenology and the niche used by a caterpillar also influence its vulnerability to insecticides. Caterpillars feeding later in the season and those that are physically protected by plant structures (*e.g.,* leaf miners or stem borers) would be less affected than free-feeding caterpillars (Faeth 1986; Leroy *et al.* 2021). At our sites, caterpillar species richness and abundance were highest in September, more than two months after the sites were treated with insecticides in 2018. Therefore, in view of the limited half-lives of the insecticides used, their application early in the season may have limited their impact on species that feed later in the season. Another explanation for the absence of late-season effect in the year of treatment may be that insecticides that are applied by aircraft are more concentrated in the canopy than in the understorey (Armstrong and Yule 1978; Sundaram *et al.* 1997). Because of this, treatments may affect caterpillars feeding in the canopy more than those feeding in the understorey.

No significant effect of insecticide treatment was observed on parasitism rates compared to those in the control sites, under the present study's conditions of low caterpillar densities. This finding indicates that host communities were not significantly impacted by insecticide treatments. In addition, parasitised caterpillars feed less than their healthy counterparts do and are therefore less likely to be affected by the insecticides (Nealis and van Frankenhuyzen 1990). However, significantly higher parasitism rates were observed after tebufenozide treatments than after *Bt*k treatments in the year of application. The higher caterpillar species richness in the *Bt*k-treated sites likely accounts for this difference, given that higher host species richness is expected to reduce the rate of parasitism (Montoya *et al.* 2003; Hillebrand and Cardinale 2004; Tylianakis *et al.* 2006). However, parasitism rates were highest at the end of the summer, when caterpillar species richness and abundance were also peaking. In this case, the higher parasitism rates may reflect the fact that many parasitoids were already within their overwintering hosts and had thus temporarily paused their development. Finally, parasitism rates also increased with spruce budworm density, which is not surprising, considering that spruce budworm was the most abundant species sampled in the present study and that its most common parasitoids represented about one-third of all parasitoid species detected (data not shown). These observations align with those of Eveleigh *et al.* (2007), who reported that densities of generalist spruce budworm parasitoids increase with that of their budworm host. Unfortunately, our data on these common spruce budworm parasitoids are too sparse to allow further analysis. Given that the insecticide

applications conducted in the present study did not significantly reduce parasitism rates, it is likely that parasitoids will maintain their natural control of spruce budworm or other species in years following treatments. This conclusion seems to be consistent with results of the ongoing programme to date.

Conclusion

In view of the results presented here, we conclude that Early Intervention Strategy insecticide applications conducted in New Brunswick neither significantly reduce nontarget caterpillar abundance nor species richness, nor do they affect their parasitism rates. Nonetheless, caterpillar species richness was higher in the *Bt*k-treated sites than in the tebufenozide-treated sites, probably because of differences in the half-lives of these two pest-control products – differences that would contribute to lingering impacts on caterpillars feeding later in the season and indirectly lead to a higher rate of parasitism in the tebufenozide-treated sites. The insecticide treatments, in a context of population control and in sites with low caterpillar abundance, reduced spruce budworm populations and did not adversely affect caterpillar species richness and abundance, thus preventing apparent competition from decreasing the natural controls on spruce budworm. The results of the present study support the hypothesis that both *Bt*k and tebufenozide, when used under the conditions described here, are well suited to maintaining low-density spruce budworm populations in the context of the Early Intervention Strategy. However, when and where high potential exists for rare or endangered nontarget species to co-occur in forests where spruce budworm might be treated, caterpillar communities should be monitored carefully to detect and mitigate any negative impacts of either *Bt*k or tebufenozide treatments.

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